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Determining Movement Patterns in Marine Organisms: Comparison of Methods Tested on Penaeid Shrimp

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Abstract.—Spatial and temporal variations in fishing effort are consistently ignored or overlooked as factors that influence patterns of recapture of tagged organisms. Perceived directional movement or migration of populations of recaptured organisms thus may be incorrect. We compared several analytical methods while trying to interpret recaptures of brown shrimp *Penaeus aztecus* and pink shrimp *P. duorarum* marked and released in 1986. Experiments were conducted off southern Texas, USA, and northern Tamaulipas, Mexico. Most recaptures were recorded north and south of release sites (alongshore), rather than east or west (offshore or inshore). Octant analysis (direction only) indicated strong southward movement of brown shrimp and pink shrimp off Tamaulipas, and equally strong northward and southward movements off Texas for both species. Analysis of mean vector angles (direction plus distance) indicated southward movement of both species off Tamaulipas but easterly movement off Texas. Recaptures per unit fishing effort indicated significant northward movement of pink shrimp only off Tamaulipas, which reflected the nonuniform distribution of fishing effort around release sites. We recommend that studies of movements of tagged organisms account for variations in fishing effort.

Mark–recapture studies of aquatic organisms are used to estimate stock range, growth, mortality, and movements. The latter topic is the subject of this article. Analyses of movements occasionally are used to relate animal distribution to an international border (Sheridan et al. 1987), to an artificial border derived from a management strategy (Booth 1979; Gitschlag 1986), or to a series of fisheries that may or may not be harvesting the same stock (Ruello 1975; Winters and Beckett 1978; Moore and McFarlane 1984). Quite often, though, the objectives of mark–recapture studies are poorly defined variations of the phrase "to investigate movements of species A off locale B." This in itself is a major shortcoming of many of the mark–recapture studies reviewed for this article.

Another serious deficiency of tagging reports is a general lack of an experimental design that can address factors that influence recapture patterns. Perhaps this stems from ill-defined objectives, yet these are mensurative experiments (Hurlbert 1984) and should be treated as such. One factor often not addressed is time; many analyses incorporate all recaptures regardless of how much time has elapsed (weeks, months, years) since the release of tagged animals. Environmental conditions change at least seasonally, and certain physical characteristics such as bottom water temperature or direction of current flow may affect directional movement. A second factor that influences recapture patterns and thus evidence for movement or migration is the effort devoted to recapture, whether it be commercial fishing or fishery-independent sampling. Catch and effort are either ignored or presumed to be uniform in time and space, which certainly is not the case for commercial fisheries. Among 29 articles we surveyed, we identified four categories of mark–recapture studies, based on consideration of recapture effort (Table 1): (1) no mention of catch or effort, (2) recognition of nonuniform catch and effort but no use of catch statistics, (3) presentation of limited catch statistics but little or no direct use of such data in interpreting recaptures, and (4) direct use of such catch statistics as recaptures per unit landings or per unit effort. The researchers used five general methods to document or prove directional movement: (1) maps illustrating release and recapture locations, often connected by straight lines or curves (which we term "connect the dots"), (2) reference to number or percentage of total recaptures in compass octants or

TABLE 1.—Selected mark–recapture studies grouped by their use of catch statistics (1–4), and by how they documented movement or migration (C = "connect the dots"; O = number or percent in octants or sectors; V = vector and circular statistics; A = analysis of variance analogue; R = recaptures per unit effort or per unit landings).

(1) No mention of fishery-dependent or -independent catch per effort
Kroger and Guthrie (1973)—C
Moores et al. (1975)—C
Oesterling (1976)—C
Ruello (1977)—C
Uzmann et al. (1977)—C
Glaister (1978)—C
Winters and Beckett (1978)—C
Booth (1979)—C
Davis and Dodrill (1979)—C
Annala (1981)—C
Cody and Fuls (1981)—O
Lyon and Boudreaux (1983)—C
Munro and Therriault (1983)—C
Moore and MacFarlane (1984)—C
Underwood and Chapman (1985)—A
(2) Nonuniform catch per effort recognized but no use of catch statistics
Jones (1959)—V
Saila and Flowers (1968)—V
Gotshall (1978)—O
Fogarty et al. (1980)—V
Bennett and Brown (1983)—V
Campbell and Stasko (1985)—V
(3) Catch statistics presented but little or no use of them
Ruello (1975)—C
Phillips (1983)—C
Somers and Kirkwood (1984)—O
(4) Catch statistics presented and used
Bayliff and Rothschild (1974)—V,R
Bayliff (1979)—V,R
Wheeler and Winters (1984)—R
Gitschlag (1986)—R
Sheridan et al. (1987)—R

other areal divisions, (3) use of vectors and vector angles, (4) analysis of variance (ANOVA) analogues, and (5) recaptures per unit landings or per unit effort.

The objective of our study was to compare tests for directional movement of marked animals across an international border. We used three methods on a single data set. Our mark–recapture experiment, conducted in 1986, dealt with brown shrimp *Penaeus aztecus* and pink shrimp *P. duorarum* native to the adjoining states of Texas (USA) and Tamaulipas (Mexico) in the western Gulf of Mexico. The U.S. National Marine Fisheries Service (NMFS) and Mexico's Instituto Nacional de la Pesca (INP) cooperated in this research.

Methods

Collection and tagging of shrimp.—Shrimp were collected by trawl at night off the Texas and Tamaulipas coasts. All collections were made in 16–20-m water depths within 5 km of release sites. Shrimp were held in flowthrough tanks before and after tagging and until they were released.

Shrimp were marked with colored, numbered polyethylene streamer tags as described by Marullo et al. (1976). Shrimp between 80 and 140 mm, total length, were selected because these sizes represented new recruits to the fishery. Tagged shrimp were released at 18-m depths within 12 h of collection from expendable, delayed-release canisters (Emiliani 1971). Each plastic canister was weighted, filled with 50–75 tagged shrimp, sealed with a salt block, and released overboard. The salt block dissolved after being underwater 10 to 15 min, and the canister sprang open, releasing the shrimp on the sea floor.

Ten releases of tagged shrimp were made at eight sites between 24°44′N 97°31′W and 25°57′N 97°04′W off Tamaulipas. These releases were made during 30 May–8 June 1986 from the INP ship *BIP-IX*. Twelve releases were made at six sites between 26°05′N 97°05′W and 26°55′N 97°17′W off Texas. The Texas releases were made during 21–27 June 1986 and 7–11 July 1986 from the National Oceanic and Atmospheric Administration ships *Chapman* and *Oregon II*. The order of release sites was randomized given the following restrictions: the 21 June release site was fixed because of vessel cruising speed, and each Texas site was visited once before visits to any site were repeated (this was not possible off Tamaulipas). Releases were confined to sites within 150 km of the USA–Mexico border (25°57′N), based on shrimp movement speeds that averaged 2.5 km/d during 1978–1980 (our unpublished data) over a maximum 60-d closure of the fishery. Following the 1978–1980 experiments, 90% of all transborder recaptures resulted from releases within 120 km of the border (Sheridan et al. 1987).

Collection of recaptured shrimp and fishing information.—Port agents employed by NMFS and INP interviewed commercial fishermen and processors in U.S. and Mexican ports to collect recaptured shrimp and information on fishing locations, landings, and effort. All recaptures during the period 30 May–31 August 1986 were checked for accuracy of date and location and were identified to species and measured (total length) when possible. Although recaptures were made after 31 August, only recaptures during the 94-d reference period were analyzed to best reflect summer environments. Recaptures returned with the following inconsistencies were omitted from analyses of movement: (1) recaptures were not identified as brown shrimp or pink shrimp, (2) recapture dates were after 31 August 1986, (3) recapture dates were prior to or the same as release dates, (4) incomplete latitude and longitude coordinates were given, (5) no depth information was available, (6) recapture date was inaccurate, (7) sex was not specified, or (8) shrimp were recaptured in trawl tows over distances exceeding 9 km. These restrictions reduced the number of usable recaptures from 5,639 (as of the date of last recapture, 5 December 1986) to 3,032.

Interviews of fishermen by port agents throughout the U.S. waters of the Gulf of Mexico were used to estimate total brown shrimp and pink shrimp fishing effort off Texas during the period 1 June–31 August 1986. These data were collected by 9-m depth zones within squares of 1° latitude and longitude, which is too coarse a scale for detailed examination of shrimp movements. Logbooks were voluntarily kept by captains of 47 Texas shrimp vessels for the duration of the recapture period; the logs contained precise information on starting and stopping points and times, depths, tow durations, and landings. Logbook data were assumed to reflect fishing activities of all vessels off Texas and were used to estimate the total brown shrimp fishing effort (which includes pink shrimp) within grids measuring 10 minutes of latitude by 10 minutes of longitude along the Texas coast.

Port agents in Tamaulipas interviewed all vessels returning to the primary port of Tampico. An unknown amount, presumed to be relatively small, of catch and effort may have been reported in more southerly ports. The interviews compiled catch and effort data by depth and 10-minute lines of latitude between 26 and 20°N (Tamaulipas and Veracruz). These data were then used to calculate effort within grids, as was done off Texas.

Data analysis.—To evaluate directional movement of brown shrimp and pink shrimp, we employed three methods: octant analysis, vector analysis, and recaptures per unit fishing effort. For octant analysis, uniform fishing effort around each release site (in time and in space) and straight-line movement from release site to recapture site are assumed. The 360° compass was divided into 45° octants with midpoints of 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° (N, NE, E, SE, S, SW, W, and NW). The compass heading for each recapture was calculated and assigned to one of these octants. The hypothesis that shrimp moved equally into all octants, which would indicate no directional movement, was tested by χ^2 analysis ($P_\alpha = 0.05$; Batschalet 1965).

Vector analysis also requires assumptions of uniform fishing effort and straight-line movement. The following descriptors of net movement of a population of tagged shrimp were calculated according to Jones (1959).

Mean vector angle (degrees from true north):

$$\bar{\theta} = \arctan \frac{\Sigma r \sin \theta}{\Sigma\, r \cos \theta};$$

north-south component (km/d, positive = north):

$$V = \frac{\Sigma r \cos \theta}{\Sigma t};$$

east–west component (km/d, positive = east):

$$V' = \frac{\Sigma r\ sin\ \theta}{\Sigma t};$$

Rayleigh test (for uniform circular distribution):

$$Z = R^2/n;$$

r = distance traveled from release site;
θ = direction traveled from release site;
t = days before recapture;
R = $[(\Sigma \sin \theta)^2 + (\Sigma \cos \theta)^2]^{1/2}$;
n = number of recaptures.

The Rayleigh test for uniform circular distributions (i.e., no preferred direction) was used to test these data (Saila and Flowers 1968).

We also tested differences in shrimp movement away from release sites by examining patterns in recaptures per unit fishing effort (R/f), which correct for temporal and spatial variations in fishing effort around each release site and integrate the effects of distance and direction traveled. For each release, recaptures per 10^4 h of effort after each release date were calculated north, within, and south of the release grid. "North" was defined as all grids lying between the northern latitude of the release grid and the northern latitude of the grid containing the northernmost recapture. "South" was defined as all grids lying between the southern latitude of the release grid and the southern latitude of the grid containing the southernmost recapture. "Within" was defined as the release grid and all grids directly east and west of it (recaptures in these grids did not show alongshore movement). Two-factor, mixed-model ANOVA with balanced cell sizes was used to test the hypothesis that there

TABLE 2.—Octant analysis of 1986 brown shrimp mark–recapture experiments. Significant differences from expected uniform distributions were tested by χ^2 analysis (** indicates $P_\alpha < 0.001$). Sites are numbered from south to north.

Release area and date	Site	Number recaptured in compass octant								χ^2
		N	NE	E	SE	S	SW	W	NW	
Tamaulipas										
May 30	6			1		7	5			
May 31	4	17	11		8	28	12			
Jun 1	5	11	7	1		21	6			
Jun 2	8	1	6	10	2			1		
Jun 3	1	5	1	2	1	30	2			
Jun 4	2		10	12	8	8				
Jun 5	3	1	9	9	10	29	6			
Jun 6	3		7	7	15	48	3			
Jun 7	5	1	14			3	14			
Jun 8	7		1			3				
Total		36	66	42	44	187	48	1	0	455.74**
Texas										
Jun 21	6				1	4				
Jun 22	2	11	1		1	9		5		
Jun 23	4	1	1		2	5			1	
Jun 24	5	9	5	2						
Jun 25	1	21	16	16	5	1				
Jun 26	3	26	24	24	31	22			2	
Jun 27	4	2	1		1	2				
Jul 7	3	10	5	8	4	3	1			
Jul 8	5		2	1	2	20				
Jul 9	1	67	13	13	11	5		10	6	
Jul 10	2	16	8	4	13	13	5		9	
Jul 11	6	16	24	22	26	72				
Total		179	100	90	97	136	6	15	38	300.61**

were no detectable differences in shrimp recapture patterns for each species off each state as indicated by *R/f* values. This was a randomized, complete-blocks design for paired comparisons of *R/f* values as fixed treatments (north or south) and for releases of tagged shrimp (10 releases off Tamaulipas, 12 off Texas) as randomly chosen blocks (Sokal and Rohlf 1969; Underwood 1981).

Results

Octant Analysis

Octant analysis indicated that brown shrimp exhibited strong southward movement off Tamaulipas (8 of 10 releases), as did pink shrimp (7 of 10 releases) (Tables 2, 3). Both brown shrimp and pink shrimp exhibited nearly equal northward and southward movement off Texas (Tables 2, 3). Chi-square analyses all indicated unequal directional movement for pooled data. Octant analysis was useful in pointing out that the distribution of recaptures may not have been unimodal (recaptures after Texas releases), and that some directions may not have been followed by shrimp before they were recaptured (W and NW off Tamaulipas; SW, W, and NW off Texas). Shrimp preferred alongshore movement and showed no trend of returning to shallower waters.

Brown shrimp and pink shrimp released on the same dates tended to move in the same directions before recapture, more so for Tamaulipas releases (7 of 10 with both species heading southward) than for Texas releases (7 of 12). Releases in the same grid location on different dates indicated that different cohorts of both species did not necessarily move in similar directions. Among the two duplicated releases off Tamaulipas (at sites 3 and 5) and six duplicated releases off Texas (at sites 1–6), brown shrimp exhibited similar directional movements in five of the eight cases, whereas pink shrimp moved similarly in only three comparisons.

Vector Analysis

Mean vector angles after 10 Tamaulipas releases indicated preferred southerly movements for both brown shrimp (in 7 cases) and pink shrimp (in 8 cases). After 12 Texas releases, equal north and south movements were indicated for both species (Table 4). Rayleigh tests indicated that not all releases were followed by significant

TABLE 3.—Octant analysis of 1986 pink shrimp mark–recapture experiments. Significant differences from expected uniform distributions were tested by χ^2 analysis (** indicates $P_\alpha < 0.001$). Sites are numbered from south to north.

Release area and date	Site	Number recaptured in compass octant								
		N	NE	E	SE	S	SW	W	NW	χ^2
Tamaulipas										
May 30	6	1	4	1		29	49			
May 31	4	6	4			6	9		1	
Jun 1	5	2				1				
Jun 2	8	1								
Jun 3	1	1	3			10	1			
Jun 4	2		3	1		1				
Jun 5	3		7	15	9	23	2			
Jun 6	3		3	2	5	15	1			
Jun 7	5	4	14			26	33			
Jun 8	7	1	6	6	1	33	3			
Total		16	44	25	15	144	98		1	435.61**
Texas										
Jun 21	6	10	1	2	13	63	12	6	1	
Jun 22	2	94	1	4	10	96	7	31	18	
Jun 23	4	70	32	10	14	89	8	10	102	
Jun 24	5	48	9		1	1			6	
Jun 25	1	94	142	65	24	85			14	
Jun 26	3	9	4	1	4	3				
Jun 27	4	40	12	14	10	38	2	10	62	
Jul 7	3	4	2	1	1	3				
Jul 8	5		5	2					11	
Jul 9	1	73	2	1	3		4		1	
Jul 10	2	24	19	4	1	12		10	10	
Jul 11	6	1	1	1	4	2				
Total		467	230	105	85	392	33	67	225	885.31**

nonuniform directional movement. Over all releases, shrimp released in Tamaulipas waters exhibited significant southward movement, and shrimp released in Texas waters exhibited net eastward movement. These trends were detected by octant analysis.

Brown shrimp and pink shrimp released on the same dates tended more strongly to move in similar directions off Texas (9 of 12 releases) than off Tamaulipas (6 of 10 releases). This is a reversal of the trends noted by octant analysis. Releases in the same grid on different dates again indicated that cohorts do not necessarily move in similar directions. Only five of eight repeated brown shrimp releases and four of eight repeated pink shrimp releases resulted in mean vector angles within 45° of each other. These results are comparable to those from octant analysis.

R/f Analysis

Analysis of recaptures per unit fishing effort indicated northward movement by pink shrimp (8 of 10 releases) but not by brown shrimp (5 of 10 releases) off Tamaulipas, whereas Texas releases were followed by southward movement after 9 of 12 brown shrimp releases and only 6 of 12 pink shrimp releases (Table 5). These results differed from both octant and vector analyses. Over all releases, however, ANOVA tests indicated no detectable differences in north versus south *R/f* values for brown shrimp off either state or for pink shrimp off Texas. Only pink shrimp released off Tamaulipas exhibited significant directional movement (northward).

Brown shrimp and pink shrimp released on the same dates tended to move in similar directions, according to *R/f* analyses (7 of 10 Tamaulipas releases, 9 of 12 Texas releases). Similar results were noted from vector analyses but not from octant analyses. Releases in the same grid on different dates resulted in different cohorts moving in opposite directions after two of eight brown shrimp releases and four of eight pink shrimp releases. All three tests indicated this result.

Comparison of Methods

Octant and vector analyses yielded similar results (southward movement) for shrimp released in Tamaulipas, but *R/f* analyses indicated no net movement for brown shrimp and northward movement for pink shrimp (Table 6). In Texas, however, each analysis indicated a different result: for both

TABLE 4.—Vector analysis of 1986 brown shrimp and pink shrimp mark–recapture experiments off Tamaulipas and Texas. $\bar{\theta}$ = mean vector angle (degrees) from magnetic north; V, V' = directed movement (km/d) in north–south and east–west components, respectively (positive values are north and east); Z = Rayleigh test statistic for uniform circular distribution of recaptures (* indicates $P_\alpha < 0.05$). Sites are numbered from south to north.

Release area and date	Site	Brown shrimp $\bar{\theta}$	Brown shrimp V	Brown shrimp V'	Brown shrimp Z	Pink shrimp $\bar{\theta}$	Pink shrimp V	Pink shrimp V'	Pink shrimp Z
Tamaulipas									
May 30	6	200.5	−1.51	−0.57	9.68*	201.7	−1.16	−0.46	58.73*
May 31	4	90.5	−0.01	0.15	5.32*	182.8	−0.79	−0.04	0.72
Jun 1	5	163.0	−0.32	0.10	2.77	18.1	1.42	0.47	0.33
Jun 2	8	64.8	0.69	1.46	12.81*	349.0	3.14	−0.61	1.00
Jun 3	1	174.9	−0.56	0.05	16.00*	167.5	−0.45	0.10	3.19*
Jun 4	2	100.8	−0.08	0.44	18.62*	153.7	−0.43	0.21	1.67
Jun 5	3	168.1	−0.50	0.11	233.34*	153.0	−0.51	0.26	20.69*
Jun 6	3	168.0	−0.49	0.10	37.37*	170.2	−0.61	0.11	11.33*
Jun 7	5	193.3	−1.58	−0.37	4.43*	196.5	−2.96	−0.88	22.66*
Jun 8	7	191.5	−1.14	−0.23	1.23	195.1	−3.17	−0.86	16.56*
Total		167.1	−0.45	0.10	84.21*	191.9	−1.30	−0.27	100.94*
Texas									
Jun 21	6	165.6	−1.02	0.26	4.90*	166.8	−1.38	0.32	45.26*
Jun 22	2	336.6	0.64	−0.28	1.84	329.6	0.49	−0.29	18.57*
Jun 23	4	154.2	−0.74	0.36	2.52	160.1	−0.42	0.15	10.27*
Jun 24	5	38.4	0.30	0.24	12.85*	23.4	1.06	0.46	50.95*
Jun 25	1	29.2	0.86	0.48	30.84*	57.3	0.24	0.38	109.27*
Jun 26	3	66.5	−0.09	0.20	228.66*	350.7	0.77	−0.13	2.49
Jun 27	4	145.5	−0.33	0.21	0.60	164.8	−0.54	0.15	12.13*
Jul 7	3	70.9	0.04	0.10	7.92*	163.7	0.33	0.09	1.30
Jul 8	5	148.9	−0.04	0.01	13.31*	15.6	0.22	0.06	8.38*
Jul 9	1	21.6	0.32	0.13	43.67*	358.1	0.38	−0.01	58.84*
Jul 10	2	357.1	0.55	−0.03	0.44	352.6	0.27	−0.14	13.42*
Jul 11	6	153.6	−1.22	0.60	54.99*	157.2	−1.29	0.54	3.83*
Total		111.8	−0.10	0.26	64.30*	111.7	−0.05	0.14	55.98*

species, northward movement by octant analysis, offshore movement by vector analysis (essentially no net north or south trend), and no net movement by R/f analysis. Yet recaptures after any given release date indicated that brown shrimp and pink shrimp tended to move in the same direction regardless of analytical method. These results suggest that shrimp in Tamaulipas waters were not subjected to the same factors that influence recapture as shrimp in Texas waters.

Discussion

Comparison of the three methods commonly employed to detect and describe animal movements or migrations revealed serious differences in results due to violations of underlying assumptions. Both octant analysis and vector analysis assumed uniform fishing effort in time and space as well as equal likelihood of movement in any direction. Catch and effort, however, are not uniform, either on a small scale around release sites for short periods of time (Somers and Kirkwood 1984; Gitschlag 1986), or along the length of a fishing ground (Sheridan et al. 1987). An examination of the distribution of fishing effort along the Texas and Tamaulipas coasts during this study period (our unpublished data) indicated that the Tamaulipas effort was only 13% of the Texas effort; further, the Tamaulipas effort was concentrated around estuary passes or river mouths, whereas the Texas effort was spread in diffuse bands paralleling the coast. Fishing effort thus has a critical influence on movement patterns that are estimated from recaptures by fishing fleets. One way to avoid this problem may be to recapture all tagged organisms. Underwood and Chapman (1985) did so to delineate factors influencing gastropod movements in rocky intertidal habitats. Their method requires the presumption that marked organisms do not move far or fast, and thus it has limited application. However, effort is expended even in collecting intertidal gastropods, and there may be differences in effort necessary to locate tagged organisms in variable rocky intertidal areas.

Octant analysis suggested that marked organisms may not be equally likely to move in any direction (because very few recaptures were made inshore of the release sites), and that directional distributions may not be unimodal. The use of chi-square and Rayleigh tests is thus of dubious

TABLE 5.—Analysis of recaptures of brown shrimp and pink shrimp per 10^4 h of fishing effort (R/f) north and south of 1986 release grids. Significant differences between paired north and south R/f values (north = south?) were tested by analysis of variance (ANOVA). Sites are numbered from south to north.

Release area and date	Site	Brown shrimp R/f North	Brown shrimp R/f South	Pink shrimp R/f North	Pink shrimp R/f South
Tamaulipas					
May 30	6	0.0	3.4	23.3	11.0
May 31	4	63.2	11.3	24.8	2.0
Jun 1	5	46.0	11.1	5.4	0.7
Jun 2	8	3.7	0.0	0.1	0.0
Jun 3	1	2.7	23.1	1.7	7.2
Jun 4	2	5.9	7.2	2.2	0.5
Jun 5	3	3.2	15.1	11.7	13.8
Jun 6	3	13.7	13.9	7.8	4.9
Jun 7	5	38.0	9.3	48.9	16.0
Jun 8	7	8.1	1.8	48.4	11.2
ANOVA		$P_\alpha = 0.25$		$P_\alpha = 0.05$	
Texas					
Jun 21	6	0.0	1.2	1.0	6.9
Jun 22	2	1.9	6.2	10.8	83.3
Jun 23	4	0.7	1.4	13.4	17.0
Jun 24	5	0.8	0.0	1.9	0.5
Jun 25	1	2.0	6.4	20.8	515.5
Jun 26	3	2.9	13.7	2.3	0.0
Jun 27	4	1.1	0.6	18.7	10.2
Jul 7	3	0.9	2.0	0.0	1.4
Jul 8	5	10.6	0.6	3.7	0.0
Jul 9	1	9.4	16.7	64.3	0.0
Jul 10	2	1.8	48.0	3.5	6.0
Jul 11	6	3.3	15.4	0.8	0.7
ANOVA		$P_\alpha = 0.14$		$P_\alpha = 0.34$	

value. Directional movement of organisms marked and released on a flat, featureless plain could be tested with either statistic. In reality, organisms are faced with shorelines, depth gradients, substrate variations, and other features that physically and physiologically prevent equal distribution in all directions. This study was conducted on newly recruited shrimp, which are not known to return to estuaries (Sheridan et al. 1987), so the presumption of equal likelihood for movement was negated.

The Rayleigh test statistic can detect unimodal distribution of recaptures away from an expected uniform circular distribution (Batschalet 1965). Octant analysis indicated that the distributions of recaptures in this experiment usually were bimodal, which reflected alongshore movement both north and south of release sites. Bimodality can be corrected but only if the modes are separated by 180° (Batschalet 1965), and such was not always the case along the curving Texas–Tamaulipas coastline. Use of the Rayleigh test in this study was thus inappropriate and could have led to wrong conclusions—e.g., that there was one preferred direction when actually there were two, as noted for Texas brown shrimp and pink shrimp. Similar problems in interpretation could result from the use of the mean vector angle.

To our knowledge, only one other article (Sheridan et al. 1987) has employed statistical testing of the octant analysis method. The authors suggested that better methods were available (recaptures per unit landings) and that octant analysis should be restricted to qualitative investigations of directional movement. Use of octant analysis to make a definitive statement on preferred movements is likely to result in error.

The use of mean vector angles and the associated Rayleigh test has lent some statistical credence to analyses based on them. Each author employing them, however, has added a qualifier to the effect that the results of mark–recapture experiments would be affected by nonuniform distribution of fishing activity around the release sites (Jones 1959; Saila and Flowers 1968; Bayliff and Rothschild 1974; Bayliff 1979; Fogarty et al.

TABLE 6.—Comparison of directional movements of marked brown shrimp and pink shrimp after their release as indicated by octant, vector, and R/f (recaptures per 10^4 h of effort) analyses. For octant and vector analyses, north includes compass headings from 292.5° to 067.4°, east includes 067.5° to 112.4°, south includes from 112.5° to 247.4°, and west includes 247.5° to 292.4°.

Release area	Preferred direction	Brown shrimp releases Octant	Brown shrimp releases Vector	Brown shrimp releases R/f	Pink shrimp releases Octant	Pink shrimp releases Vector	Pink shrimp releases R/f
Tamaulipas	North	1	0	5	3	2	8
	South	8	7	5	7	8	2
	East–west	1	3	0	0	0	0
	Net	South	South	None	South	South	North
Texas	North	6	6	3	9	7	6
	South	4	5	9	2	5	6
	East–west	2	1	0	1	0	0
	Net	North	East	None	North	East	None

1980; Bennett and Brown 1983; Campbell and Stasko 1985). Thus the need to collect, analyze, and use fishery statistics has been recognized for many years without being regularly incorporated into experimental designs. Fogarty et al. (1980) also presented Rayleigh test statistics indicating that recaptured American lobsters *Homarus americanus* released near barriers (coastlines of rivers, bays, and sounds) invariably exhibited directional movement away from the barriers, but that recaptured lobsters released on the open continental shelf where there were no physiological or physical barriers exhibited no significant directional movement. The assumptions necessary to uphold judgments based on vector analysis (uniform fishing activity and equal likelihood of directional movement) are thus lacking in many coastal fisheries.

We recommend adjusting recapture data by effort or landings; we prefer effort over landings because organisms usually are not uniformly distributed in space (one unit of landings does not equal one unit of effort). Wheeler and Winters (1984) used recaptures and recaptures per unit landings to document the return of Atlantic herring *Clupea harengus harengus* to spawn near bays where they were marked and released. Because effort data were not available, Wheeler and Winters assumed that one unit of catch required the same effort in all bay areas. Their results indicated that recaptures alone did not document the capacity of spawning Atlantic herring to return to their home bays. Only recaptures per unit landings indicated a pattern of declining recapture rates with increasing distance from tagging sites. Homing intensity was nearly 90% for spawning herring. Consequently, it was postulated that management of a spawning group could prevent overfishing to extinction. Because of the high degree of homing, repopulation would only occur by straying from adjacent spawning grounds.

Sheridan et al. (1987) also used recaptures per unit landings, in this case to address possible losses of brown shrimp and pink shrimp from U.S. commercial harvest because of movements across the USA–Mexico border in the Gulf of Mexico. They used landings to adjust tag returns because effort was not available for the entire study period. Their analysis indicated that brown shrimp tended to move south after release in waters of both countries and that pink shrimp had a variable response. Their study primarily addressed long-distance, prolonged returns over a wide range of latitudes and seasons, whereas our work has been more focused and short-term in nature.

Bayliff and Rothschild (1974) and Bayliff (1979) reported migratory patterns of yellowfin tuna *Thunnus albacares* in terms of recaptures weighted by fishing effort in the eastern Pacific Ocean (Mexico to Ecuador). No preference for offshore movement with growth was noted, but a tendency for southerly movement was noted during spring months. However, the tagging results were not tested for directional movement after individual releases, and interpretation of those results could have been confounded by the long recapture periods (up to 1 year after each release) and the large areas of ocean surface addressed (0–25°N, 80–150°W). Gitschlag (1986) employed recaptures per unit effort to assess movements of pink shrimp near the Tortugas Sanctuary, a management area off southwest Florida in which shrimp fishing is prohibited. Pink shrimp recruited to commercial fishing grounds instead of moving into untrawlable or protected waters where they would be lost to the fishery. Our *R/f* analyses will be used to investigate potential losses to the U.S. shrimp fishery from shrimp movements during and after the closed fishing season off Texas.

In conclusion, recapture data should be adjusted for fishing effort when they are used to determine movement patterns of species comprising commercial or recreational fisheries. The added expense for data collection would be offset by improvements in the quality of the results.

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